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THE SPAWNING HABITS OF THE SEA LAMPREY, PETROMYZON MARINUS[1]

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THE spawning habits of several species of lamprey are known from observations which have been made in both Europe and America.[2] Those of the sea lamprey, *Petromyzon marinus,* however, have not been studied, notwithstanding that this is the largest of the lampreys and is common to both sides of the Atlantic. It is merely known that this species ascends rivers for the purpose of spawning; and that the "fish" transport stones in building their nest much like other lampreys (Burroughs, '83; Holder, '85). In 1883 a French observer, L. Ferry ('83), noted the development of sea lamprey eggs taken directly from a female specimen. He concluded that the eggs must already have been fertilized, and hence that fertilization in the lampreys is internal. This conclusion, in the light of the careful observations on the spawning of various lampreys, especially *Petromyzon planeri* and *Lampetra wilderi,* is undoubtedly erroneous. Moreover, the discovery that lamprey eggs can develop parthenogenetically (Bataillon, '03), affords a simple explanation of the facts recorded by Ferry. None the less the observation of the breeding habits of the sea lamprey was very desirable.

The observations recorded in this paper were made by the writer on Long Island, June 1 and 2, 1911, while collecting material for a group to represent the nesting habits of the sea lamprey in the American Museum of Natural History. The locality, Smithtown, on the Nissequogue River, Long Island, was suggested to me by

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[1] Read before the American Society of Zoologists, at Princeton, N. J., Dec. 27, 1911.

[2] See annotated bibliography at end of paper.

Professor Bashford Dean, who had learnt of it through Dr. Tarleton H. Bean.

Locality and Date of Observation.—At the date of these observations, June 1 and 2, 1911, lampreys had been seen in the Nissequogue River for several days. A number of abandoned, partly scattered nests were also to be found; hence June 1, appears to be toward the end of the spawning season, which for Long Island must be put down as the latter half of May.

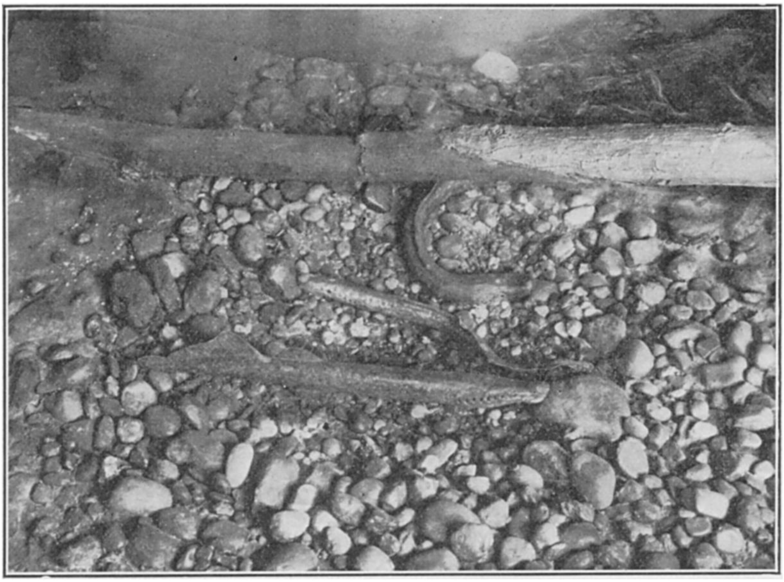

FIG. 1. SEA LAMPREYS, *Petromyzon marinus*, ON A NEST. An exhibition group, 4 by 5 feet, in the American Museum of Natural History; prepared under the supervision of the writer.

The Nissequogue is a small stream which empties into Long Island Sound. At the village of Smithtown, three and a half miles from its mouth, it is shallow (a foot or two deep), perfectly clear, and flows over a bed of large, water-stained pebbles. Here and there are patches of "river grass." The water is perfectly fresh here, although still affected by the tide. A quarter of a mile above and below the village bridge, the river grows deeper and muddier; my observations were therefore confined to the pebbly portion, a stretch of about half a mile. Here a dozen nests were found, four with lampreys on them, the others deserted and partly scattered by the tide.

Nests.—The nest of the sea lamprey is similar to that of other species, but much larger. It is a circular depression in the river bed, two to three feet in diameter. One that was measured was two feet three inches across, and six inches deep in the center. The nests are easily recognized, even at a distance of several feet, by the large number of whitish quartz pebbles which have been uprooted and turned with their clean faces up. They are built at random anywhere in the river: near the bank, in the shade of overhanging trees; in the middle of the stream, exposed to the glare of the sun; or even, as with the nest shown in the figures

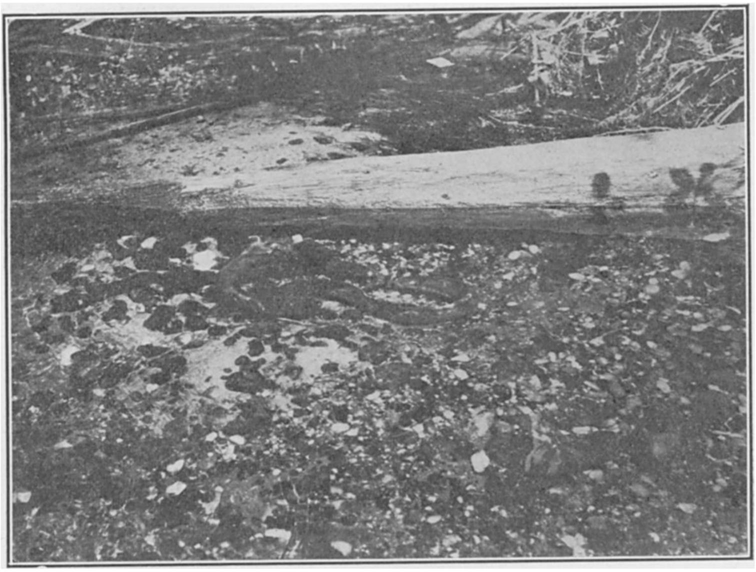

FIG. 2. THREE SPECIMENS OF *Petromyzon marinus* ON A NEST. Instantaneous photograph taken without special apparatus in bright sunlight, at low tide, with only three or four inches of water above the "fish." One male and two females. (Not retouched.)

(Figs. 1 and 4), partly under a log. Occasionally two nests adjoin so that their peripheries overlap.

Standing in the water close to a nest, one may observe minutely every movement the lampreys make. One may even stroke them or lift them by the tail without disturbing them. A "fish" must be raised to a considerable angle before it will loosen its hold on the stone to which it clings, and dart away; and then it will go only a short distance, fifty or a hundred feet, and seek refuge under the "river grass."

The manner of building the nest is quite like that of the brook lamprey (*Lampetra wilderi*), as described by Gage ('93), and by Dean and Sumner ('97). But owing to the large size of the species all the processes are writ large, as it were, so that one can see the purpose of every movement. Building the nest consists in carrying the pebbles and stones out of a circular area until a basin-like depression is formed. As the work proceeds the finer material in the interstices between the pebbles gradually accumulates, so that the bottom of the nest becomes covered with sand and fine gravel. The stones are seized with the circular mouth to which they cling entirely by suction. The "teeth" play no part in this work, as may be proved by experimenting with the freshly dead "fish." By pressing the mouth of such a "fish" against a stone, it may be made to hold on so tenaciously, that by lifting the stone one lifts the fish (Fig. 3). A vacuum is produced inside the buccal funnel, and this is the immediate cause of the hold. In carrying stones out of the nest, the procedure varies with the size of the stone. Small stones, an inch or two across, are picked up in the

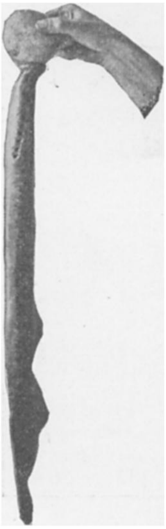

FIG. 3. Freshly dead lamprey clinging to a stone by the vacuum produced in the buccal funnel when the mouth is pressed against it.

mouth and carried out. Larger stones, firmly rooted in the bottom, require considerable effort to be dislodged; the stone is tugged upward, the lamprey receding backward in a straight line. Sometimes instead of pulling backward, the lamprey charges head-on and pushes the stone in front of it up the incline, the body remaining rigid and acting as a lever, while the tail is lashed violently to gain a firmer support. Some of the larger stones carried by the lampreys out of the nest (Fig. 4), were picked up just as they were released from the mouth; they were found to weigh (in air) from 145 to 840 grams.

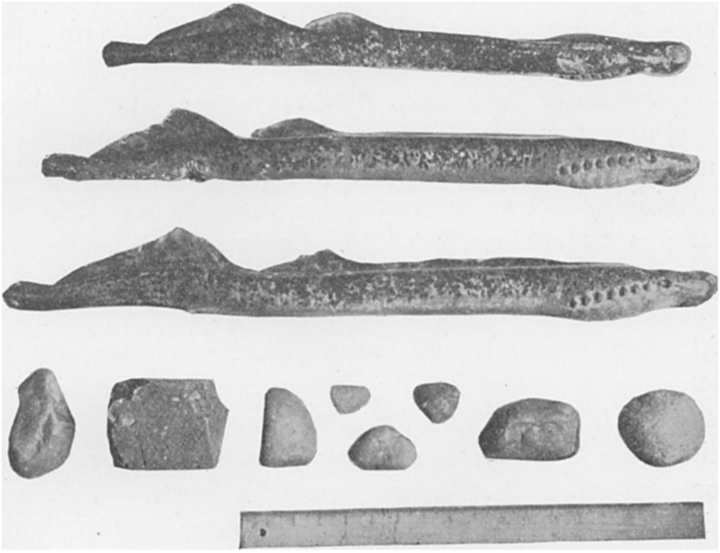

FIG. 4. SAME THREE SPECIMENS AS SHOWN IN FIG. 2, PHOTOGRAPHED SHORTLY AFTER THEY WERE TAKEN FROM THE NEST. Upper two, females; lowest one, a male. The stones in lower half of photograph were picked up just as they were carried by the lampreys out of the nest. The half brick shown in the picture weighs 840 grams.

The building and improving of the nest go on continuously between intervals of mating. Both the male and the female take part in this work. On one nest there were observed a male and a female; they were joined now and then, for some minutes, by a second female which had been for some time by herself on an adjoining nest. During the time the three "fish" were on the one nest (Figs. 2 and 5) they all took part in repairing it, in the intervals between mating—the male apparently not distinguishing between the female of his own nest and the intruder. In two other cases there was one individual to a nest. After carrying a stone out the lamprey immediately returns for another. This is repeated a number of times and then the lamprey clings to a stone apparently exhausted (Fig. 4). Now and then the tail is lashed against the sides of the nest to pad it down. When on a nest by itself, a lamprey occasionally wanders a distance of some feet—even several hundred feet—but invariably returns to continue its nest-building. These wanderings are perhaps for the purpose of finding a mate.

Mating.—The method of copulation is similar to that of the brook lamprey, *Lampetra wilderi,* as described by Dean and Summer ('97); and it is unnecessary to redescribe it here. I will merely comment on a few details. The female must cling to a large stone in the nest in order that copulation take place. The male seizes her by the top of the head. *In copulo,* the two are arranged so as to form an ellipse. The caudal portion of the male is applied immediately back of the first dorsal of the female, and curved in a loop around her body. Several authors have referred, in the case of both American and European lampreys, to the vibration of the posterior portions of the "fish," *in copulo.* In the sea lamprey this vibration may be observed very closely. It lasts two or three seconds. It begins slowly, gradually increases in frequency until it reaches an exceeding rapidity of vibration, then subsides by a few slow beats. The motion strongly suggests the vibration of a rattlesnake's tail in the warning pose. Indeed while watching the lampreys one can hardly keep from imagining the sound which *ought* to accompany the lampreys' vibrations, so similar is the movement to that of the rattlesnake's tail.

As to the length of time "fish" on a nest continue to spawn, I was able to make some observations. The nest shown in Figs. 1 and 4 was observed continuously for over four hours, from 10 A.M. until after 2 P.M.; and during that time copulation took place at intervals of from a few to ten minutes; and in all probability would have continued several hours longer had the "fish" been left on the nest. Both became gradually more and more scarred from seizing each other with their mouths: round pale wounds stood out clearly against the blue-black of the head of the female where the male had repeatedly seized her; and large whitish wounds could be seen on her back, especially posterior to the first dorsal fin. The male likewise was scarred in several places on the head and back. These scars are

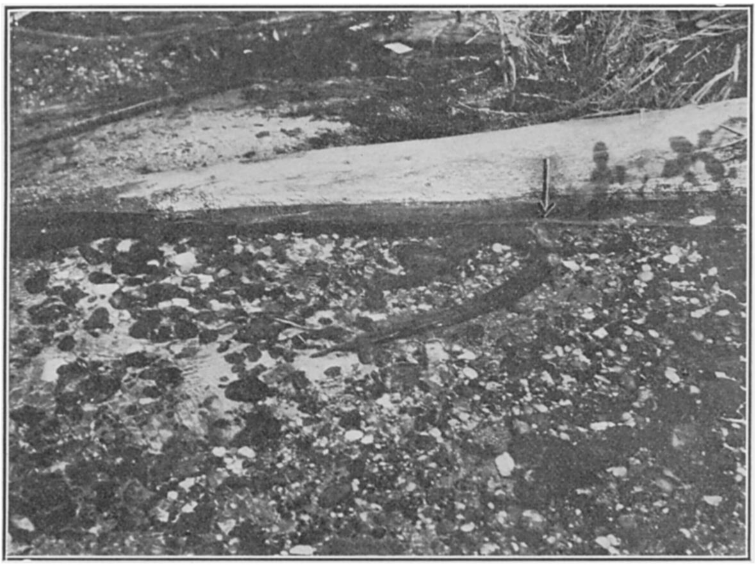

FIG. 5. THE SAME NEST AS IN FIG. 2, SHOWING TWO OF THE SPECIMENS *in copulo*. The head of the male is seen protruding from under the log directly under the arrow; his body is hidden by the log and his tail is looped around the female. The second female is seen clinging to a stone. (Not retouched.)

greatly augmented through continual rubbing against stones, padding down the nest, etc.

Fate of Sea Lampreys After Spawning.—From the facts at hand, it appears that lampreys that go up the river to spawn do not again return to the sea, but die shortly after spawning. I found two dead, badly scarred, spent lampreys in the river not far from deserted nests. One was in the shade of tall grass near the bank, the other tangled in weeds and twigs in the middle of the river. Both had been rasped, apparently for food, by other lampreys. Burroughs ('83), also records that it is not unusual to find dead lampreys in June.

The causes of the death of these lampreys—and indeed of all anadromous fishes—are still rather obscure. Death is probably chiefly due to the cycle of katabolic processes initiated on the maturing of the gonadial products. Besides this at least two other causes must be regarded as contributary: first the greatly lessened vitality due to the constant exertion in uprooting and transporting stones. Lampreys thus weakened become the prey of other lampreys. Secondly, the numerous scars or wounds which they inflict on one another in mating allow "fungus" to invade, and ultimately to destroy, their tissues. All three of these causes, probably, play a part in causing the death of the sea lampreys after spawning.

Remarks on the Senses and Mentality of the Sea Lamprey.—The behavior of the lampreys was carefully noted to see in how far their senses come into play in building the nest and in other activities. The general impression was that the sea lamprey is guided by touch more than by any other sense. Sound does not disturb them while on the nest: one may carry on a conversation right over a nest without in the least affecting them. Indeed one lamprey that was building a nest under a wooden bridge was not disturbed by the clattering of automobiles over it. This insensitiveness to sound may mean, however, merely absorption in the work of nest-building, and not that the lampreys are insensible to this stimulus.

The eyes of lampreys in the water shine like black beads; but they are not very sensitive. If one meets a lamprey swimming toward him in the river, it will come almost right up before it will discover the person and turn aside.

Many of the movements of the sea lamprey on the nest are purposeless—as was noted also for the brook lamprey by Dean and Summer ('97). Thus a lamprey will sometimes pick up a stone outside the nest, carry and drop it into the nest; or while carrying out a stone, will drop it half way up the side of the nest. It will tug at a large stone which it cannot possibly dislodge, or at a log, in an effort to drag it out of the nest, and will repeat this again and again, without profiting in the least by previous failures. On the whole one has a feeling that the lamprey possesses a very low mentality even as compared with fishes.

ANNOTATED BIBLIOGRAPHY

The following list includes all the papers I have been able to find that deal with the spawning habits of lampreys. Those having to do with the cytology of fertilization are listed in Ziegler's text-book referred to below.

Bataillon, E.

1903. La segmentation parthénogénétique expérimentale chez les œufs de *Petromyzon planeri*. *Comp. Rend. Acad. Sci.*, Vol. 137, pp. 79–80.

Carried embryos as far as the blastula stage—''*en plongeant et maintenant les œufs* dans des solutions de saccharose à 5 ou 6 pour 100 ou dans des solutions isotoniques de NaCl.''

Burroughs, John.

1883. A lamprey's nest. *The Century Magazine,* XXV, p. 457.

Observed *Petromyzon marinus* spawning in a creek. Describes their mode of transporting stones; their indifference to an observer at close range; but does not describe the nest, nor apparently recognizes the purpose for which the stones are transported. The female is the larger of the two. ''In June it is not unusual to find their dead bodies in the streams they inhabit.''

Dean, Bashford, and Sumner, Francis B.

1897. Notes on the spawning habits of the brook lamprey (*Petromyzon wilderi*). *Trans. N. Y. Acad. Sci.*, XVI, pp. 321–324, Pl. XXVII.

Detailed observations on manner of building nest, on copulation, and general behavior. Contains the best figure extant of lampreys on nest.

Ferry, L.

1883. Sur la lamproie marine. *Compt. Rend. Acad. Sci.*, pp. 721–723. Translated, in part, in *Ann. Mag. Nat. Hist.*, (5), II, p. 388 (May, 1883).

A female sea lamprey, taken by a fisherman while clinging to his boat, was opened, and its ova put into a large basin. It rained at the time and the basin became partly filled with water. After twenty days the eggs hatched into perfect larvæ. Ferry concludes: ''Il resort de ce fait que les œufs pris dans le ventre de la Lamproie étaient déjà fécondés et avaient dû l'être dans l'intérieur de l'animal'' (p. 722).

Gage, Simon H., and Meek, Seth E.

1886. The lampreys of Cayuga Lake (abstract). *Proc. Amer. Assoc. Adv. Sci.*, XXXV, p. 269.

Brief reference to nests and to length of breeding season, which is said to last nearly two months (May and June).

Gage, Simon H.

1893. The lake and brook lampreys of New York, especially those of Cayuga and Seneca Lakes. *The Wilder Quarter-Century Book.* Ithaca. Pp. 421–493, Pls. I–VII.

Gives extended account of nest building and spawning of the brook lamprey (*Lampetra wilderi*) and of the lake lamprey (*Petromyzon marinus unicolor*); discusses fate of lampreys after spawning (pp. 441–447). Figures two lake lampreys on a nest, carrying stones—Pl. vii, Fig. 39.

Herfort, Karl.

1901. Die Reifung und Befruchtung des Eies von *Petromyzon fluviatilis. Arch. f. mikrosk. Anat. u. Entwickl.*, Vol. 57, pp. 54–95, Pls. iv–vi.

Brief review of some European papers on spawning habits (pp. 55–57). For his own studies he fertilized the eggs artificially (pp. 57–58).

Holder, Charles Frederick.

1885. The lamprey-eel and nest. In *Marvels of Animal Life;* 8°; New York; pp. 5–8.

Describes how *Petromyzon marinus* transports stones, but mistakes the mass of stones accumulated outside the nest, for the nest itself. Quotes from an account of over fifty lampreys building near a dam in the Saco River, Maine. They dropped the stones on the dam until it became covered over. This was erroneously interpreted to mean that the lampreys had built the dam. A stone is sometimes carried by two lampreys.

Kupper, Carl v., and Benecke, B.

1878. Der Vorgang der Befruchtung am Ei der Neunaugen. *Festschrift für Theodor Schwann.* Königsberg.

Loman, J. C. C.

1910. De copulatie van *Petromyzon planeri. Tijdschr. nederl. dierk.* Vereen, (2), XII, p. vii.

A careful account of the spawning of *Petromyzon planeri,* observed in a brook near Königsberg.

McClure, Charles F. W.

1893. Notes on the early stages of segmentation in *Petromyzon marinus* L. (*americanus* Le S.). *Zool. Anz.,* XVI, pp. 367–368; 373–376.

Collected thirty specimens from a river near Princeton, New Jersey, between May 20 and June 1.

Müller, August.

1856. Ueber die Entwickelung der Neunaugen. Ein vorläufiger Bericht. *Arch. f. Anatomie, Physiol. u. wissen. Medicin,* Jahrg. 1856, pp. 323–339.

This is the earliest account of the breeding habits of the lamprey. The observations were made on the brook lamprey; sometimes ten or more were seen together tugging at, and transporting stones. The object for which the stones were carried was, however, not made out. He made the discovery, by rearing Ammocœtes, that they are the larvæ of lampreys.

Reighard, Jacob.

1903. An experimental study of the spawning behavior of *Lampetra wilderi. Science,* N. S., XVII, p. 529 (abstract).

No constant relation between individual fish and indivdual nests. Location of nest is determined not by character of bottom, but by ''existence beneath or in the midst of the running water of small masses of water at rest,'' *e. g.,* in depressions or in vicinity of obstructions.

1908. Photography of aquatic animals in their natural environment. *Bull. U. S. Bureau Fisheries,* XXVII, pp. 43–68, Pls. iii–v.

Photograph of four *Lampetra wilderi* on a nest—Pl. iii, Fig. 2.

Vejdovsky, F.

1893. O trenī mihule (*Petromyzon planeri*) [Die äussere Befruchtung des Neunauges]. *Sitzber. d königl. böhm. Gesell. Wiss. in Prag. Math.-naturw.,* 1893, article XLIX, Pl. xviii.

Observed spawning process in an aquarium containing four males and one female. Figures two specimens (Pl. xviii) *in copulo,* but this figure does not represent them in their characteristic attitudes.

Vieira, Lopes

1831. Remarks on the eggs and spawning-season of *Petromyzon fluviatilis* Linn. *Ann. de Sciencias Naturæs,* I, pp. 79–83.

Sea lamprey enters rivers of Portugal at end of December and beginning of January.

Yarrell, W.

1831. Remarks on the Eggs and Spawning-season of *Petromyzon fluviatilis* and *P. marinus*. *Proc. Committee of Sci. and Corresp. Zool. Soc. London,* Part I, pp. 133–134.

Examined specimens of *P. fluviatilis* weekly from March to middle of May. Up to April 19, there were more females than males; thereafter males outnumbered females, two to one. Specimens taken April 26, appeared ready to spawn. By May 10, nearly all examined had spawned. Seven specimens of *P. marinus* were taken in the Severn on May 3—"about which time they ascended that river for the purpose of spawning."

Young, Robert T., and Cole, Leon J.

1900. On the nesting habits of the brook lamprey (*Lampetra wilderi*). *Amer. Naturalist,* XXXIV, pp. 617–620.

Notes on nesting observed in two small tributaries of the Huron River near Ann Arbor, Michigan. Males precede females in beginning the nest. Nests are 7½ inches in diameter and situated anywhere in river.

Ziegler, Heinrich Ernst.

1902. Lehrbuch der vergleichenden Entwickelungsgeschichte der niederen Wirbeltiere.

Résumé (pp. 74–75), and bibliography (pp. 74, 89–91).